

THE BIOLOGY AND HOSTS OF *PROCECIDOCHARES ATRA* (DIPTERA: TEPHRITIDAE): EVIDENCE FOR CRYPTIC SPECIES?¹

T. Keith Philips², D. Courtney Smith³

ABSTRACT: Galls of *Procecidochares atra* on *Solidago* in late spring contained an average of 15.3 ± 5.1 gregarious larvae ($n = 3$). Previous records note only monothalamous galls for this species. Twenty-one larvae were found in one gall whereas the previous maximum number of larvae per gall in the genus was 13. Our spring record indicates that *P. atra* is bivoltine, uncommon for a temperate species of fruit fly. We also note new records of *Solidago canadensis* and *Erigeron canadensis* as hosts and a *Eurytoma* species (Hymenoptera: Eurytomidae) as a parasitoid of *P. atra*. The possibility that our collections represent undescribed cryptic species of *Procecidochares* closely related to *P. atra* is discussed.

Most species of *Procecidochares* Hendel cause galls on composite plants. Galls form either in the stems or in the flowers of hosts (Benjamin 1934). One known exception is the non-galling *P. flavipes* Aldrich, which reproduces in flower heads (Goeden et al. 1994). Eleven species have been described in this genus in North America north of Mexico (Foote et al. 1993). *Procecidochares atra* (Loew) is one of the largest and most commonly collected species in the eastern United States and ranges from Florida to Nova Scotia and West to Utah and Idaho. Only monothalamous galls (i.e., galls which contain single larvae) in late summer are known in this species (Felt 1918, Phillips 1946, Philips and Smith, unpublished). Published hosts include several species of *Solidago* Linnaeus and an undetermined species of *Aster* Linnaeus (Wasbauer 1972) with the latter record questionable (Foote et al. 1993). Here, we report the occurrence of galls where the larvae develop gregariously within a single gall; our observations represent the largest number of larvae per gall reported in the genus. We also discuss the probability of a bivoltine life cycle and note two new hosts for, and a parasitoid of, *P. atra*.

METHODS

Galls were collected in Franklin County, Ohio. Two galls on an undetermined *Solidago* species were collected on 8 May, 1991. One of these galls was dissected. A third gall on *Solidago canadensis* Linnaeus was collected two years later on the 14 May, 1993. A single gall growing on *Erigeron canadensis* Linnaeus was found in August 1992. All larvae or pupae were allowed to com-

¹ Received July 30, 1997. Accepted October 5, 1997.

² Department of Entomology, Museum of Biological Diversity, Ohio State University, 1315 Kinnear Road, Columbus, Ohio 43212.

³ Department of Entomology, Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210.

plete development to adult stage in the laboratory. Twelve galls on *Solidago canadensis* were collected in early September, 1996. These galls were dissected and number of puparia per gall counted. Pupae were also examined for evidence of parasitism. The single parasitoid discovered was allowed to emerge and then killed for identification. Voucher specimens from both plant hosts, the parasitoid, and *Solidago* galls from one of the May collections and the September collection are deposited in the Ohio State University Insect Collection and the United States National Museum. Adults which emerged from *Solidago* are also in the authors' collections.

RESULTS

The three late spring *Solidago* galls were found two to four inches above the surface of the ground at the apical meristem. The first two galls collected in 1991 contained 14 and 21 pupae. Adults emerged from five to 11 days after collection (13-19 May) with the majority (25 of 33 flies) emerging from the 14-16 May. Two flies failed to eclose. The third gall collected in 1993 contained 11 pupae. All adults successfully eclosed (but dates of emergence were not recorded). This third gall (in a dry state) measured 25-30 mm in length by 9 mm in width. The average number of larvae per spring *Solidago* gall was 15.3 ± 5.1 ($n = 3$). Larvae develop gregariously in each gall, without separate compartments for each individual.

Galls on *Solidago canadensis* collected in September were all monothalamous. Each contained a single, empty puparium except for two of them. One produced a parasitoid in the genus *Eurytoma* Illiger (Hymenoptera: Eurytomidae) and the other held a partially eclosed, dead *P. atra*. All late summer *Solidago* galls were situated approximately midway or higher on the plant stalk on apical meristems. Both the late spring and late summer *Solidago* galls were composed of swollen tissue surrounded by leaves in a typical rosette growth form.

A single gall collected on *Erigeron canadensis* in August contained only one larva which eclosed in late August or early September. The *Erigeron* gall was a swollen stem approximately two inches above the ground.

DISCUSSION

Several species of *Procecidochares* produce galls containing single larvae. Examples include *P. atra* (Felt 1918, Phillips 1946), *P. minuta* (Snow) (Novak et al. 1967), *P. stonei* Blanc and Foote (Tauber and Tauber 1968) and various species in the literature without precise identities (Silverman and Goeden 1980, Wangberg 1980). In other species, one to several larvae develop within a single gall. Wangberg (1980) usually found one to three larvae but recorded up to six in his *Procecidochares* sp. "B" and from one to seven (recorded in table 1) for *Procecidochares* sp. "C." Stegmaier (1968) found *P. australis* Aldrich galls

contained two to eight larvae per gall. Similarly, Phillips (1946) found this species to have up to eight, but most often had only a single larva per gall. Bess and Haramoto (1958) record an average of three larvae in each gall of *P. utilis* Stone. The highest reported number of larvae in a single gall is 13 in *P. stonei* (Green et al. 1993). But the average for this species was only 2.5 ± 0.1 larvae per gall. By comparison, in spring galls we found up to 21 larvae of *P. atra* in a single gall and an average of 15.3 ± 5.1 ($n = 3$) larvae or pupae per gall. Published biologies of *P. atra* are not explicit on the number of larvae per gall or the life cycle. For example, Felt (1918) lists a small rosette gall containing a single larval cell on *Solidago altissima* and refers to two species, *P. polita* (Loew) and *P. atra* (as *Oedaspis polita* and *O. atra*). He cites Stebbins (1910), but she only mentions *P. polita* and not *P. atra*. Felt (1918) either had his own records or may have listed both species because they are sympatric in Massachusetts, where Stebbins (1910) based her study. Phillips (1946) studied two larvae of *P. atra* taken from goldenrod galls, implying a single larva per gall. Galls we collected on *Solidago canadensis* in late summer contained only single puparia but, as previously mentioned, galls collected in late spring produced an average of 15.3 ± 5.1 ($n = 3$) larvae or pupae.

The number of larvae per gall can vary within a species depending upon the host. *Procecidochares stonei*, when living in *Virguiera laciniata* Gray, produces up to 13 larvae per gall (Green et al. 1993). When this same species uses *Virguiera deltoidea* Gray var. *parishii* (Greene) the maximum number of larvae per gall drops to three. For unknown reasons, the number of larvae varies seasonally even within the same host in *P. atra*. The spring generation on *Solidago* develops with large numbers of larvae per gall, whereas the fall generation, whether on *Solidago* or on *Erigeron canadensis*, occurs as a single larva per gall.

Galls with more than one larva can have two different types of internal gall structure. Polythalamous galls contain separate compartments for each larva while others are without internal divisions. Species of *Procecidochares* are known to form both types. Wangberg's (1980) *Procecidochares* sp. "C" forms polythalamous galls. In contrast, *P. stonei* larvae develop gregariously within a gall (Green et al. 1993). Our dissections showed that *P. atra* develops in galls gregariously in the spring, without separate compartments for each larva.

Most species of *Procecidochares* appear to have a limited number of hosts (Foote et al. 1993). For those species with large numbers of reported hosts, such as *P. minuta* (Snow), it appears as though sibling or cryptic species are involved (Wangberg 1980, Foote et al. 1993). Previously recorded hosts for *P. atra* are *Solidago altissima* Linnaeus, *S. nemoralis* Ait., *S. odora* Ait. and one questionable record from *Aster* (Wasbauer 1972, Foote et al. 1993). Our collections add two additional hosts, *Solidago canadensis* and *Erigeron canadensis*. *Procecidochares anthracina* (Doane) is the only species of this genus previ-

ously recorded from a species of *Erigeron*. Like *P. atra*, this species has been recorded from both *Solidago* and *Erigeron*. This is evidence that galling by one tephritid species on both of these hosts may be common. The other notable aspect of our *Erigeron* record is that the gall was located on the stem near the ground and not on an apical meristem as in *Solidago*. In light of the differences in both host plant and gall location, we initially thought the *Erigeron* galler represented a different species. But we are unable to differentiate this specimen morphologically from other specimens of *P. atra*.

Procecidochares atra adult emergence from galls in late spring and late summer indicate a bivoltine life cycle, whereas most temperate species of tephritids have only one generation per year (Bateman 1972, Christenson and Foote 1960). There are other species of *Procecidochares* that are bivoltine or even multivoltine. *Procecidochares utilis*, a species native to Mexico, has two generations per year (Hoy 1960). The *Procecidochares* sp. of Silverman and Goeden (1980) is bivoltine in Southern California, although it is sometimes univoltine and conceivably even biennial if adequate rainfall, which triggers necessary vegetative regrowth, does not occur. Huettel and Bush (1972) mention both *P. australis* and an undescribed *Procecidochares* species as multivoltine. These two species emerge in the fall from galls in flower heads. The adults then oviposit in small, overwintering rosette plants. Larvae and their galls develop slowly over the winter and the spring generation emerges from these plants. Our records of *Procecidochares atra* suggest a similar life cycle, except that adults may overwinter and oviposit on the perennial *Solidago* as new shoots emerge in the spring. Most temperate species of fruit flies overwinter as diapausing pupae (Bateman 1972).

Biological records for some *Procecidochares* species are questionable because of the need for systematic revision of the genus. Incomplete taxonomy has resulted in species listed by letter designations (Wangberg 1980) or species listed as near a described taxon (Dodson 1986, 1987). Even with *P. atra*, which could be considered a well-known species, there is potential for cryptic species. As evidence, Foote et al. (1993) mention that specimens of *P. atra* from the western part of the range have only one pair of dorsocentral bristles. The more typical pattern is two pairs, with one pair anterior to and the other posterior to the transverse suture. Although two pairs is the more common pattern, we found this character to be extremely variable in our specimens reared from the late spring galls. Almost half of our specimens have three or four setae anterior to the suture (in addition to the posterior pair) and more rarely a single pair anterior and two pairs of setae posterior to the suture.

Regardless of the morphological variability in *P. atra*, it is clear that our May records from *Solidago* are not for another described species. The only *Procecidochares* that use *Solidago* as a host are *P. anthracina*, *P. minuta*, and *P. polita*. Of these, only *P. polita* (Loew) is an eastern species, and although

about the same size as *P. atra*, both are relatively easy to differentiate (see Foote et al. 1993). One possibility is that our May records are for a new cryptic species temporally separated from *P. atra*. Our record on *Erigeron* may even represent a second new species. Similar to the situation described by Huettel and Bush (1972), the species may have differentiated in their host plant use, but have not diverged morphologically, even though they exist sympatrically. Genetic studies may be useful in determining if our records represent a single bivoltine species with two hosts, two separate species with possibly different hosts, or even three species.

ACKNOWLEDGMENTS

We foremost thank George Keeney for his collection of the spring galls and his information on the host species and gall location. We also thank John Furlow for his assistance with plant identification and his discussions on *Solidago* and Andrey Sharkov for the Hymenoptera identification. Our appreciation to two anonymous reviewers whose comments greatly improved the manuscript.

LITERATURE CITED

- Bateman, M. A. 1972. The ecology of fruit flies. *Ann. Rev. of Entomol.* 17: 493-518.
- Benjamin, F. H. 1934. Descriptions of some native trypetid flies with notes on their habits. U.S. Depart. Agric. Tech. Bull. 401. 95 pp.
- Bess, H. A. and F. H. Haramoto. 1958. Biological Control of pamakani, *Eupatorium adenophorum*, in Hawaii by a tephritid gall fly, *Procecidochares utilis* l. The life history of the fly and its effectiveness in the control of the weed. *Proc. X Int. Cong. Entom.* Montreal 4: 543-548.
- Christenson L. D. and R. H. Foote. 1960. Biology of fruit flies. *Ann. Rev. Entom.* 5: 171-192.
- Dodson, G. 1986. Lek mating system and large male aggressive advantage in a gall-forming tephritid (Diptera: Tephritidae). *Ethology* 72: 99-108.
- Dodson, G. 1987. Host plant records and life history notes on New Mexico Tephritidae (Diptera). *Proc. Entomol. Soc. Wash.* 89: 607-615.
- Felt, E. P. 1918. Key to American insect galls. N. Y. State Mus. Bull. 200. 310 pp.
- Foote, R. H., F. L. Blanc, and A. L. Norrbom. 1993. Handbook of the fruit flies (Diptera: Tephritidae) of America north of Mexico. Cornell Univ. Press, Ithaca. 571 pp.
- Goeden, R.D., D.H. Headrick, and J.A. Teerink. 1994. Life history and descriptions of immature stages of *Procecidochares flavipes* Aldrich (Diptera: Tephritidae) on *Brickellia* spp. in southern California. *Proc. Entomol. Soc. Wash.* 96(2): 288-300.
- Green, J. F., D. H. Headrick, and R. D. Goeden. 1993. Life history and description of immature stages of *Procecidochares stonei* Blanc & Foote on *Viguiera* spp. in southern California (Diptera: Tephritidae). *Pan-Pac. Entomol.* 69: 18-32.
- Huettel, M. D. and G. L. Bush. 1972. The genetics of host selection and bearing on sympatric speciation in *Procecidochares* (Diptera: Tephritidae). *Entomol. Exp. Appl.* 15:465-480.
- Novak, J. A., W. B. Stoltzfus, E. J. Allen, and B. A. Foote. 1967. New host records for North American fruit flies. *Proc. Entomol. Soc. Wash.* 69: 146-148.
- Phillips, V. T. 1946. The biology and identification of trypetid larvae. *Amer. Entomol. Soc. Mem.* 12. 161 pp.
- Silverman, J. and R. D. Goeden. 1980. Life history of a fruit fly, *Procecidochares* sp., on the ragweed *Ambrosia dumosa* (Gray) Payne, in southern California (Diptera: Tephritidae). *Pan-Pac. Entomol.* 56: 283-288.
- Stebbins, F. A. 1910. Insect galls of Springfield, Massachusetts, and vicinity. *Springfield Mus. Nat. Hist. Bull.* 2. 138 pp.

- Stegmaier, C. E., Jr. 1968. *Erigeron*, a host plant genus of tephritids (Diptera). Fla. Entomol. 51: 45-50.
- Tauber, M. J. and C. A. Tauber. 1968. Biology of the gall-former *Procecidochares stonei* on a composite. Ann. Entomol. Soc. Amer. 61(2): 553-554.
- Wangberg, J. K. 1980. Comparative biology of gall-formers in the genus *Procecidochares* (Diptera: Tephritidae) on rabbitbrush in Idaho. J. Kans. Entomol. Soc. 53(2) 401-420.
- Wasbauer, M. S. 1972. An annotated host catalog of the fruit flies of America north of Mexico (Diptera: Tephritidae). Occasional Papers No. 19, Bureau of Entomology, Calif. Dept. Agric., Sacramento. 172 pp.

BOOK REVIEW

WORLD CATALOG OF ODONATA. VOLUME I, ZYGOPTERA; VOLUME II, ANISOPTERA. Henrik Steinmann. 1997. Walter de Gruyter, Berlin & New York. 1025 plus pp. \$870.00 US.

These two volumes comprise a straightforward, well-produced, and comprehensive catalog of the worldwide odonate fauna. It attempts to list all known species, arranged according to the taxonomic categories recognized in Davies and Tobin's earlier (1984, 1985) lists, except that the arrangement of Gomphidae follows Carle (1986). Taxa are listed alphabetically within each higher category (i.e., genera are alphabetical within tribes, etc). Each entry includes a fairly extensive synonymy, although not a complete bibliography of each taxon. This is especially helpful for categories above genus, for which such information often does not come easily to hand. Unfortunately, in a number of cases Steinmann cites references in Davies and Tobin as the first entry in a species synonymy rather than citing the actual original description (e.g., - "1985 *Gomphurus ozarkensis* Westfall, 1975 - loc. cit. Davies & Tobin, ..."). Taxa down to and including tribes are diagnosed briefly, although these descriptions merely repeat those of Davies and Tobin, which sometimes are not, in fact, adequately diagnostic. The type species is listed for each genus as well as the location of the type (if known) and type locality for each species. Species entries also give an indication of the geographic range, although this often is quite general or incomplete. At the end of each volume is a complete index of all names within the corresponding suborder and at the end of Vol. II a selected bibliography totaling about 600 entries (not all synonymic listings appear in the collected bibliography). A certain number of errors have crept in. The type species of *Aeshna*, e.g., is given as *Libellula vulgatissima* L. (it is actually *L. grandis*; *L. vulgatissima* is later, correctly, cited as the type of *Gomphus*), and *Pseudohagenius* is placed as a subgenus of *Hagenius* rather than of *Sieboldius*. Warts and all, this work is much as one would expect from a catalog for a medium-sized order of insects and, because it contains substantially more information than those it is intended to supersede (Davies and Tobin, 1984, 1985; Tsuda, 1991), it represents a major improvement on them. Unfortunately, it has appeared about six years too late.

I say this because the present work seems to have been done without any reference to (or awareness of ?) the excellent catalog of Bridges, first published in 1991, with the third and final edition appearing in 1994, shortly before the author's untimely death. Bridges' work was privately published, but it has been discovered by most serious students of Odonata and has been widely used and cited. It thus seems astonishing that Steinmann's books should take no account of Bridges'. Be that as it may, a comparison is certainly in order, since each work has the same general objectives and each has its strengths and weaknesses.

Bridges' catalog organizes and lists family group, genus group, and species group names, each alphabetically within separate sections. A fourth section lists species within genera; genera are again listed alphabetically, but higher classification to the level of subfamily or, when possible, tribe, is indicated in compact form after each genus. Thus Steinmann's work provides a more quickly and easily grasped overview of classification, but the process of finding entries for

(continued on page 188)